DIVE BEHAVIOR OF ADULT AND SUBADULT HARBOR SEALS FROM KODIAK ISLAND AND SOUTHEAST ALASKA

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INTRODUCTION

By providing information concerning foraging ecology (Bjorge *et al*. 1995, Tollit *et al*. 1998), energetics (Houston 1995, Coltman *et al*. 1998) and potential marine mammal and fisheries interactions (Boyd 1997, Boyd *et al*. 1998), analysis of dive behavior and movement patterns is critical to conservation and management of pinnipeds. While many studies have used time-depth recorders (TDR) to examine harbor seal (*Phoca vitulina*) dive behavior, dive behavior of harbor seals is poorly documented in Alaska at the northern portion of their range. Most studies have been conducted during the breeding season, whereas few studies have examined the diving behavior of harbor seals over an entire year (but see Frost *et al*. 2001). Satellite-linked time-depths recorders (SDR) allow dive behavior and movements to be monitored remotely, such that seals can be monitored for an entire molt cycle (one-year) (Frost *et al*. 2001). While this technology provides a longer time frame of information, difficulties in dealing with the summarized data format have been troublesome. Whereas TDRs record characteristics of individual dives (depth, duration, rates of ascent and descent, and bottom time), more limited dive behavior data is available from SDRs.

Specifically, SDRs record the number of dives in a 6-hour period within user-defined intervals for dive depth, dive duration and time-at-depth in three separate histograms.

In this chapter we examine effects of season, time-of-day, age, sex and geographic subregion using data from SDRs to better understand diving and foraging behavior of harbor seals in Alaska. Relating dive patterns to foraging effort is particularly important if we are to understand potential causes for declines in harbor seals in the Gulf of Alaska (GOA) in recent years. A severe decline (72 – 85%) in numbers of seals hauled-out on Tugidak Island (south of Kodiak Island in the western GOA; Fig. 1) occurred from the 1970s through the early 1990s (Pitcher 1990, Jemison and Pendleton 2001), yet an increasing population trend but much reduced abundance has been observed in recent years (Jemison and Pendleton 2001). Harbor seal numbers have also declined by 63% since 1984 in Prince William Sound (Frost *et al*. 1999). Severe declines in Steller sea lions (*Eumetopias jubatus*), northern fur seals (*Callorhinus ursinus*) and several seabird species have also occurred in the GOA and Bering Sea (Merrick *et al*. 1987, Trites 1992, Springer 1993). In contrast, harbor seal and Steller sea lion numbers in Southeast Alaska have increased or remained stable over the past 15 years (Small *et al.* 2001, Calkins *et al*. 1999). Although causes for declines in the GOA are not well-understood, one possible cause is reduced foraging efficiency related to declines in prey abundance and availability following extensive reorganization of the marine ecosystem after the 1977 climate regime shift in the GOA (Francis *et al*. 1998, Anderson and Piatt 1999). Comparison of foraging effort and dive patterns between seals from the GOA and those from Southeast Alaska may provide additional information concerning the role of food in the observed declines.

In this chapter we present our analyses as a work in progress. For this chapter, our main objectives were to: (1) quantify diving parameters for harbor seals in Alaska; and (2) test for significant variation in dive parameters among ages, sexes, seasons, subregions and periods of the day. We also explored novel techniques for analyzing dive data from SDRs that consider the binned-nature of SDR data, variation among individuals, and temporal auto-correlation (Frost *et al*. 2001). Our overall objective for this study, to be addressed in a forthcoming manuscript, was to compare dive parameters, and potentially foraging effort, between an area of recent population decline (Kodiak) and a region of population increase or stability (Southeast Alaska). We cannot investigate directly the role of dive behavior and foraging effort in the dramatic decline observed in the Kodiak region from 1977 to 1988 from these dive data, as the Kodiak population, though remaining much reduced from historical numbers, was increasing during the time of this study. Comparison of dive behavior between seals from Southeast Alaska and PWS may be more informative of the role of poor food conditions in harbor seal declines in the GOA since the PWS population has continued to decline at a rate of 4.6% per year between 1990 and 1997 (Frost *et al.* 1999).

METHODS

Capture Methods and Instrumentation

Seals were captured from 1993 to 1996 in Southeast Alaska and around Kodiak Island near haul-outs by entanglement in a multifilament nylon net (240 m long, 8 m deep with a 28 cm stretch mesh, and float and lead lines). Two boats and a swimmer were used to quickly deploy the net such that seals that had moved into the water when approached were surrounded. Entangled seals were quickly removed from the net, placed in temporary holding nets, and processed on a nearby beach or support vessel. Seals were immobilized using a ketamine and diazepam mixture at a dose of 5.5

mg/kg and 0.09 mg/kg, respectively. Type III SDRs (0.5 watt ST-6 transmitters manufactured by Wildlife Computers) with netting were glued to the fur mid-dorsum using quick-setting epoxy. Seals were also weighed, measured, and tagged with individually numbered tags placed in one or both hind-flippers. Seals were captured in the fall (post-molt) in all years, and in early spring (pre-molt) in 1993 and 1995.

SDR units were equipped with pressure and conductivity sensors, which sampled pressures (depths), and whether the unit was wet or dry, every 10 seconds with a projected capacity of 30,000 to 100,000 transmissions depending on the unit. Transmitters summarized dive data in histograms for four six-hour time periods (local Alaska time): 0300-0900 hr. (morning), 0900-1500 hr. (day), 1500-2100 hr. (evening) and 2100-0300 hr. (night). In 1993-1994, dive depth data were summarized in six histogram bins: 4-20 m, 21-50 m, 51-100 m, 101-150 m, 151-200 m and >200 m. Dive durations were summarized into 6 bins of 2 minutes each (where Bin 1 = 0-2 min., and Bin 6 = >10 minutes). In 1995-1996, dive depth and duration were summarized in 10 bins and data were later converted back to the 6-bin format. Ten depth bins included: 4-20 m, 21-50 m, 51-76 m, 77-100 m, 101-150 m, 151-200 m, 201-250 m, 251-300 m, 301-350 m, and >350 m. Dive durations were summarized into 10 bins of 2 minutes each (where Bin 1 = 0-2 min., and Bin 6 = >18 minutes). Time-at-depth data were only collected from SDRs deployed in 1995 and 1996. In 1995, time-at-depth was summarized for ten bins: 0 m (conductivity sensor dry; i.e. seal hauled-out or not-submerged at the surface), >0-20 m, 21-50 m, 51-76 m, 77-100 m, 101-150 m, 151-200 m, 201-250 m, 251-300 m, 301-350 m, and >350 m. In 1996, time-at-depth bins were chosen for greater sensitivity in shallow water: 0 m, >0-4 m, 5-20 m, 21-50 m, 51-76 m, 77-100 m, 101-150 m, 151-200 m, 201-250 m, and >250 m.

Data were summarized by period of day for each 24-hour period and stored in a transmit buffer which was replaced with new data every 24-hours. Also recorded was the precise maximum dive depth for each 24 hour period and total surface time (included time when the unit was dry and time when depth was 0 m) over the past two six-hour periods. The maximum depth recordable was 490 m with a depth measurement resolution of 2 meters. The maximum number of dives recordable in any bin was 255. Some transmitters were duty-cycled to transmit one-day on and two days off; others transmitted continuously. Some SDRs were programmed to suspend transmission after 6 hours dry. Locations were obtained from transmissions in which the units were able to uplink multiple times to an ARGOS satellite during one over pass. Analysis of these data to examine movements of seals are presented elsewhere (Small and Ver Hoef 2001). All locations ranked as quality ≥1 were used in data analysis (see Small and Ver Hoef 2001 for explanation of quality rankings).

Databases for each data type (depth, duration, time-at-depth) were created using SAS and databases were rigorously checked for errors against the original extraction files. To examine smaller-scale geographic variability, data of the two major regions were divided into smaller subregions based on topography and water depth: 7 for Kodiak and 9 for Southeast Alaska (Figs 1 and 2). Seals were categorized as adult (≥4 years) or subadult (<4 years) by morphometric measurements and experienced observers in the field.

Statistical Analyses

We first summarized data as the mean proportion of dives within each bin for dive depth, dive duration and time-at-depth. To do this, proportions were calculated as number of dives in bin i / total number of dives, for each histogram (where histograms tally data over a six-hour time period). Mean proportions over histograms were summarized for males, females, adults, and subadults, for both regions (Kodiak and Southeast Alaska). Mean dive frequencies and maximum dive depths were also calculated by age, sex, and region. We then defined three dive parameters for statistical tests: (1) time wet, (2) diving focus, and (3) preferred dive depth bin. *Time wet* was defined as the number of minutes a seal was submerged per six-hour period, based on time-at-depth bin 0 data when the conductivity sensor read "dry" (the number of minutes in bin 0 was subtracted from 360 to calculate time wet). Only data from SDRs deployed 1995-1996 (n = 35 individuals) when time-at-depth was recorded were used to examine *time wet*. *Time wet* was used as the initial index to diving or foraging activity because it included time spent swimming, travelling and diving in both shallow and deep water. Although other activities unrelated to foraging occur in shallow water, inclusion of data from shallow water was critical given harbor seals spend a large proportion of their time within zero to four meters of the surface (from 20 to 60% of the time during the breeding season; Coltman *et al.* 1997, Lesage *et al.* 1999, Frost *et al.* 2001), at the limit of the SDRs' resolution. There is also evidence that significant foraging occurs in water less than four meters in depth by harbor seals during the breeding season (Coltman *et al*. 1998, Lesage *et al*. 1999).

Both *focus* and *preferred depth bin* were examined using data based on two *time wet* categories: (1) "any time wet" (all data regardless of time wet) and (2) "majority time wet" (data from histograms where time wet was >180 minutes, i.e. half the data collection period). Time-at-depth information was not needed to create "any time wet" datasets, and thus the complete data set collected during 1993-1997 (n = 62 individuals) was used. In contrast, the "majority time wet" datasets required time-at-depth information, and were therefore created from the subset of records collected during 1995-1997 (n = 35 individuals). Focus and preferred depth were then examined for both of the two "time wet" datasets created. *Focus* was a quantitative measure of the diversity of depth bins used by seals, and was calculated for each histogram using the Dominance (D) parameter from Simpson's Diversity Index (Simpson 1949),

$$D = \sum_{n=1}^{6} \left(\frac{n_i (n_i - 1)}{N (N - 1)} \right) \quad (1)$$

where, n = the number of dives in bin i, and N = the total number of dives in the histogram. Focus could have ranged from 1.0 (all dives in the same bin) to 0.167 (dives evenly distributed among the six bins, given large sample sizes). Focus was primarily used as a means of conditioning data for examination of preferred depth by indicating histograms in which seals demonstrated a preference for some depth bin. Given a large sample size, a value of "D" > 0.5 resulted from a substantially larger proportion of dives occurring in one bin than other bins, given dives occurred in many bins. If dives occurred in only two bins, a value of 0.5 indicated that at least one to a few more dives occurred in one bin than the other bin. "D" was a relative measure of focus and was dependent on choice of intervals for bins. Therefore we examined focus statistically to compare focus among the regions and groups in this study, and to compare with studies in Prince William Sound, Alaska, in which bins chosen were identical to those chosen for this study (Frost *et al*. 2001). *Preferred Depth Bin* was calculated for each histogram using only data where focus (D) was > 0.5 (i.e. dives were more common in one depth bin), and defined as the depth bin with the most dives. By conditioning data on D > 0.5, we described dive depths only for periods of focused diving.

Finally, we tested for effects of age, sex, subregion, month (seasonal variation), and time period (diurnal variation) on the three dive parameters using repeated measures mixed models in SAS. To provide equal representation of all seals and reduce long computation run-times of analyses, a subset of 100 histograms from each seals' data was selected randomly. Effects of period, age, sex, month and subregion on time wet, focus and preferred depth were first examined using a forward stepwise procedure using PROC MIXED in SAS. Variables were added to the model one at a time; individual was also included in this model as a random effect. After determining the optimum model, a repeated measures model (to account for temporal autocorrelation) was used to reduce variables in the optimum model by a backward stepwise procedure, removing any non-significant variables one at a time. The random effect of seal was retained in the repeated measures models.

RESULTS

From 1993-1996, SDRs were deployed on a total of 62 adult and subadult seals from Kodiak Island and Southeast Alaska (56% from Southeast; 52% males; 69% adults; Table 1). Retention rate of SDRs, particularly those deployed post-molt in the fall, was high (Table 1). Units were operational for a median of 88 days for spring-deployed SDRs (range: 52-140) and for a median of 221 days for fall-deployed SDRs (range: 18-304)

Statistical Analyses

Summary of data indicated dive frequencies of 7.7 to 10.5 dives per hour with maximum frequencies of up to 62.5 dives per hour (Table 2). Mean and maximum dive frequencies were not significantly affected by limitations to the number of dives per bin recordable by SDRs (255 dives), because only 15 out of 24,652 histograms contained bins with 255 dives. Proportion of dives per bin ranged among groups from approximately 0.40-0.60 for depth bin 1 (4-20 m.), 0.10-0.35 for depth bin 2 (21-50 m.), 0.08-0.27 for depth bin 3 (51-100 m.), and 0.01-0.16 for depth bin 4 (>100 m.). While most dives of Kodiak seals occurred in depth bins 1 and 2, most dives of Southeast seals occurred in bins 1 and 3, with a greater proportion of dives >100 m for Southeast seals compared to Kodiak seals (Table 2). Most dives were 0-4 minutes long: 0.33-0.46 from 0-2 min, 0.22-0.45 from 2-4 min, 0.16-0.20 from 4-6 min, and 0.03-0.19 >6 min. Proportion time dry (hauled-out or not submerged) was consistent among groups ranging from 0.27 – 0.28 (Table 2). Of the time submerged, the proportion of time spent from 0-20 m was 0.62 to 0.80, either remaining in these depths or transiting through these depths to deeper or shallower waters. Consistent with depth and duration data, Southeast seals tended to spend more time at greater depths (> 51 m) than Kodiak seals (0.23 and 0.05, respectively). Of the time spent from 0-20 m in 1996, approximately 0.70-0.85 of time was spent from 0-4 m and 0.15-0.30 of time was spent from 5-20 m (Table 2). This equates to a range among groups of 0.45-0.70 of the total time submerged spent from 0-4 m, above the minimum depth programmed to monitor dive depth and duration. Maximum depth recorded for Kodiak seals was 368 m, and for Southeast seals was 508 m, at the depth limit of the SDR. Southeast seals diving deeper than 450 m were all adult males and included 8 individuals tagged in 1993 or 1994. Mean maximum depths ranged from 143.2 to 244.2 m for Southeast seals, whereas those of Kodiak seals ranged from 72.1 to 86.5 m (Table 2).

For statistical analyses, only data from subregions with the majority of data were included; specifically, Kodiak subregions KO2 (43.5%) and KO3 (47.7%), and Southeast subregions SE1 (47.5%), SE2 (30.9%), and SE8 (18.0%; Figs 1 and 2). Use of the repeated measures model was particularly appropriate for these data. After fixed effects were accounted for, temporal autocorrelation explained a greater proportion of the residual variance than individual seal, explaining 8 to 17% for time wet and focus, and 25 to 46% for preferred dive depth (Table 3).

Although effects of autocorrelation persisted for long-time periods (ranging from 10 to 53 days; Table 3), in all but one case models including and excluding temporal auto-correlation yielded identical results of significance tests. The random effect of individual seal accounted for 2 to 9% of the residual variation for time wet and focus, and 0 to 27% of residual variation for preferred dive depth (Table 3).

Time wet

Significant seasonal and diurnal variation in time wet was detected in both Kodiak and Southeast Alaska (Table 4). For both regions, time wet was generally highest from October through December, slightly lower in January through April, and decreased from May to July. For Southeast, time wet was markedly lower in July than other months (Fig. 3a). For both regions, seals spent the greatest time wet at night and the least time wet during the morning and day (Fig. 3b). By averaging the monthly proportions shown in Fig 3a, time wet averaged 0.69 in Kodiak and 0.66 in Southeast during the evening period. Relative to the evening period, this average decreased by 7.0% in the morning period for both regions (e.g., -20.125/289.331 and –17.812/258.634 from Table 4) and by 15.7% and 2.0% in the day period for Kodiak and Southeast, respectively (Fig. 3b). This average increased by 8.7% and 5.1% in the night period for Kodiak and Southeast, respectively (Table 4, Fig 3b).

Focus

Focus ranged from 0.50 to 0.80 for Kodiak seals and 0.40 to 0.65 for Southeast seals, based on a possible range of 0.167 to 1.0. Diurnal effects on diving focus were observed in both Kodiak and Southeast and in both datasets "any time wet" and "majority time wet" (Table 5). Diving was most focused during mid-day (Fig. 4a-b) when time wet was least (Fig. 3b). In Kodiak, adults, and particularly adult females were more focused than other groups (Fig. 4c). In Southeast, females were more focused than males in the greater-time-wet dataset (Fig. 4d); sex was not significant in the any-time-wet dataset. No age variation in diving focus was apparent for seals tagged in Southeast. Unlike Kodiak data, focus varied among subregions in Southeast Alaska, with higher focus in SE1 (nearshore around the coast of Admiralty Island) and SE8 (Frederick Sound), and lower focus in SE2 (nearshore around the coasts of Chichagof and Baranof Islands, Fig. 3e). Subregion differences however, were observed only in the any-time-wet dataset. Using the majority-time-wet dataset, focus increased significantly from February to July (Fig. 4d).

Seasonal variation was significant in the random model, but not the repeated measures model due to collinearity between month and subregion. Both effects were significant in the model containing only a diurnal effect. However, subregion may be the more important variable of the two because subregion was more important than month in the subregion, month model; and the subregion, time-period model was stronger than the month, time-period model.

Preferred Dive Depth Bin

Preferred depth bin ranged from bins 2.0 to 2.5 (or from 21-75 m) for Kodiak seals and 2.0 to 4.0 for Southeast seals (or from 21-150 m, Fig. 5). Age effects on preferred depth bin were significant for both datasets for the Kodiak data (Table 6). Whereas adults dived slightly deeper than subadults in the majority-time-wet dataset, subadults dived deeper than adults in the any-time-wet dataset (Fig. 5a); no age effects were apparent in Southeast. Southeast seals dived deepest in late winter (December through February) with decreasing dive depths observed through spring (February through June) and into summer with shallowest dives in May and June, before increased depths were observed again in fall (Fig. 5c); no significant seasonal effects were apparent in Kodiak. Only in the Southeast any-time-wet dataset were diurnal effects on preferred dive depth apparent (Table 6), in which dives were deepest during the evening hours (Fig. 5b).

DISCUSSION

Diving and haul-out behavior of harbor seals in Alaska

In this study we present new data documenting dive behavior of Alaskan harbor seals for comparison with other studies. The proportion of time seals spent hauled-out (or not submerged at the waters surface) increased from 0.20 - 0.30 during the winter and spring to 0.40 – 0.50 during the breeding season, when all ages and sexes were more likely to be hauled-out (Fig. 3a). A VHF monitoring study on Tugidak Island found a similar seasonal pattern in proportion time hauled-out for "resident" seals (not seen at a site other than Tugidak Island) with proportions higher in the breeding season (0.50 of days) than the fall (0.41 of days; Pitcher and McAllister 1981). Harbor seals from Prince William Sound also spent more time hauled-out during the breeding season than during the winter, though the proportion time hauled-out during winter (< 0.20) may be lower than that for Kodiak and Southeast seals (0.20 – 0.35; Fig 3a), and the seasonal effect greater (Frost *et al*. 2001). Other studies report proportion time hauled-out during the breeding season ranged among individuals from 0.07 to 0.39 (Moray Firth, Scotland; Thompson *et al*. 1998) and averaged 0.45 and 0.60 for adult females and pups respectively (Sable Island, Canada, Bowen *et al*. 1999).

Most dives were between zero and four minutes long for both Kodiak and Southeast Alaska, which is similar to average dive durations of harbor seals from TDR (2.5 minutes, Fedak *et al*. 1988; 3.7 minutes, Stewart and Yochem 1994; 3.3 minutes, Bjorge *et al*. 1995) and VHF studies (median submergence time ranged 0.8 to 2.9 minutes over individuals, Ries *et al*. 1997). Other studies report maximum dive durations for harbor seals of 10.3 minutes (Stewart and Yochem 1994), 14.3 minutes (Bjorge *et al*. 1995) and 5.8 minutes (for lactating females during the pupping season, Boness *et al*. 1994) from TDR studies and 31 minutes from VHF studies (Ries *et al*. 1997). Although maximum dive duration is not recorded by SDRs, this study recorded 939 out of 666,902 dives (0.001) greater than 18 minutes in length.

This study has documented some of the deepest dives made by harbor seals with maximum dive depths to 508 meters, at the limit of the measurement capabilities of the SDR. While TDR studies of harbor seals document maximum dives of 60 to over 200 meters (Boness *et al*. 1994, Bjorge *et al*. 1995, Coltman *et al*. 1997, Tollit *et al*. 1998, Lesage *et al*. 1999), several studies have documented dives to nearly 500 meters (446 meters, Stewart and Yochem 1994; 480 meters, Frost *et al*. 2001). Kolb and Norris (1982) document remains of a harbor seal in a sablefish trap at a depth of 558 ± 40 meters. Harbor seals are physiologically capable of making dives to over 500 meters but do so rarely because of either foraging preferences or physiological, energetic or ecological constraints. As documented by other studies, harbor seals from this study were shallow divers with nearly 50% of dives from 4-20 meters in depth, and 98% and 87% of dives less than 100 meters in depth for Kodiak and Southeast seals, respectively (Table 2). Estimates of average preferred depth bin from the mixed model analysis (Fig. 5) were deeper than those suggested by patterns observed using mean proportion dives per bin (Table 2). Proportions were highest in bin 1 (5-20 meters) for both groups, while the second highest proportion was observed from 21-50 meters (bin2) for Kodiak seals versus 51-100 meters (bin 3) for Southeast seals. In contrast, preferred depth bin ranged from 2.0 to 2.5 for Kodiak seals (21-50 to 51-75 meters) and from 2.0 to 4.0 (21-50 to 101-150 meters) for Southeast seals. This apparent discrepancy may result from conditioning the data used to estimate preferred depth bin on focused diving, or from patterns that only emerge once individual variation and temporal autocorrelation are accounted for. Preferred dive depths of seals from Prince William Sound ranged from 21-75 meters and were therefore similar to dive depths used by Kodiak seals (Frost *et al*. 2001).

Variation in dive parameters among age and sex groups included greater focus for adult females than other groups for Kodiak seals; and greater focus for females than males for Southeast seals during times of greater time wet. A similar pattern was observed in Prince William Sound, where diving of adult females was significantly more focused than other groups (Frost *et al*. 2001). For Kodiak seals, adults accessed deeper water than subadults did during periods of greater time wet; whereas subadults accessed deeper water than adults did when all data, regardless of time wet, were considered (Fig. 5a). This may indicate that adults dive deeper than subadults at Kodiak only during periods when they are submerged a majority of the time, presumably when they are foraging or diving more actively.

Diurnal variation in dive behavior included a greater probability of being hauled-out during the morning and daytime than evening and nighttime periods, and greatest focus during the day. Nearly identical diurnal patterns were observed in time wet and focus for Prince William Sound seals (Frost *et al*. 2001). A tendency for harbor seals to haul-out more frequently during the day than the night was also observed in Froan Nature Reserve, Norway (Bjorge *et al*. 1995). No evidence for seals feeding on vertically migrating prey was observed in this study, as no diurnal effect on dive depth was observed for Kodiak seals and the preferred depth bin for Southeast seals was deepest during the evening period and shallowest during the day and night. Lack of diurnal effect on dive depth supports the hypothesis that harbor seals feed predominantly on benthic prey (Bjorge *et al*. 1995, Tollit *et al*. 1998, Lesage *et al*. 1999). Other studies have reported a preference of harbor seals for foraging during evening hours. Lesage *et al*. (1999) detected more U-shaped, potentially foraging dives (types 1 and 3) during dusk. However, Lesage *et al*. (1999) also found evidence for seals feeding on vertically migrating prey because the deeper version of the U-shaped dive (type 1) was performed more often than the shallower version (type 3) during twilight than during night. Seals may prefer to forage during twilight because prey is more densely clumped during dawn and dusk than during night and day (Lesage *et al*. 1999). Lactating harbor seals from Sable Island, Canada also dove more frequently in the night and early morning, with no significant diurnal variation in dive depth or duration (Bowen *et al*. 1999).

Nearshore bathymetry and habitat characteristics likely play large roles in shaping dive behavior of harbor seals (Bjorge *et al*. 1995) because harbor seals generally forage within 50 km of haul-outs (Thompson 1993, Tollit *et al*. 1998) and tend to be benthic feeders (Tollit *et al*. 1998, Lesage *et al*. 1999). Patterns in dive behavior may reflect movement patterns and water depths available to seals, rather than prey preferences or differing foraging strategies unrelated to choice of foraging area. Effects of bathymetry are probably most evident when comparing regional differences in this study. For example, greater maximum dive depths and greater proportion of dives in deeper depth and duration bins for Southeast than for Kodiak seals (Table 2), likely reflected the deeper waters available nearshore for Southeast seals and bathymetric constraints on Kodiak seals. Ranging out 2 km from the coastline around Kodiak Island (subregions KO2 and KO3, included 91.2% of locations), the majority of water depths range from 20 to 100 meters, and up to 250 meters. Near-shore waters are much deeper in Southeast, particularly off the east coast of Chichagof and Baranof

Islands (SE2; commonly ranging from 150 to 450 m, up to 750 m) and the west coast of Admiralty Island (SE1; ranging from 100 to 350 m, up to > 600 m). Water depths in Frederick Sound (SE8) commonly range from 100 to 300 m, and up to > 450 m (Fig. 2).

The regional differences in dive parameters suggested by the results of this study, have a seasonal component. Deeper dive depths and decreased dive focus for Southeast relative to Kodiak seals occurred mainly during the winter months, while dive behavior during the breeding season appeared similar between the two regions. The inverse relationship between focus and depth is expected because focus will generally increase when seals are concentrated near shallow waters in this study. For example, because of the depth bins chosen in this study, only one or two shallow-water depth bins were available to seals. Increased focus and shallower diving during summer compared to winter may result from active selection of shallower water by seals in the summer principally to participate in breeding activities, rather than restricted movement patterns during the summer. In contrast to other studies (Thompson *et al*. 1994, Van Parijs *et al*. 1997, Tracey Gotthardt *unpublished data*), harbor seals from both Southeast and Kodiak have *less* restricted home ranges and move greater cumulative distances in the summer than the winter (Small and Ver Hoef 2001). This suggests seals may prefer to forage in deeper waters when they are not limited by the need to participate in breeding activities, or that seals follow seasonal movement patterns of prey. Collinearity between the variables month and subregion in mixed models suggest that although Southeast seals have more restricted home ranges in winter, they forage in different areas (most likely with deeper water) during the winter than during the summer.

Comments on the statistical analysis

We used a repeated measures model to account for effects of temporal auto-correlation and included individual seal, an often important factor in explaining dive behavior (Bjorge *et al*. 1995, Burns *et al*. 1997), in statistical models. We did not calculate mean dive depths in this study but instead characterized dive behavior, including dive depths and variability in dive depths used by seals, through the variables, "focus" and "preferred dive depth bin". Using these variables allowed us to address dive depths and variability in dive depths without assuming a frequency distribution of dive depths within a bin. Some studies calculated mean dive parameters from SDR data by using the mid-point depth of bins and therefore assume normal distributions within bins. Although a study of Weddell seals has shown that differences between mean depth per bin from TDR records and the mid-points of bins chosen for SDRs were small (2 – 11%) this result likely depends on how well bins matched the behavior of the species studied (Burns and Castellini 1998). When bin widths are large as in this study, depth and duration profiles are likely to be asymmetrical within bins such that the mid-point may be a poor estimator of average dive performance. Moreover, only in light of "focused" dives does a "preferred" depth make sense. Conditioning dive depth on focus therefore excludes histograms with poor estimates of "average" dive depth.

Potential disadvantages to using "dive focus" and "preferred depth" include difficulties in interpreting parameter estimates and in comparing results to other studies. The focus "D" criteria of 0.5 used in this study was liberal and allowed more data to be retained for analysis (reduction of only 11 to 29% of data). However, interpretation of "D" is less clear for values of D in the middle of the range of possible values (i.e., 0.4 - 0.6). Mid-range values of D result from many possible scenarios which at the extreme include: (1) at least one more data point in one bin, when data occur in only two bins; or (2) many more data in one bin when data are in several bins, when sample sizes are large. If data are in mainly two bins, "D" does not describe whether these are adjacent or non-adjacent bins. Therefore biological interpretation of "D" is difficult for mid-range values but "D" is useful as a conditioning tool, when dive parameters of "focused" diving are desired. Likewise, estimates of preferred depth bin are difficult to relate to true dive depth values from TDR data. A preferred depth of 1.5 indicates that on average, seals dove to 1.5 bin-units. By assuming a distribution of depths within a bin, we could equate this to approximately 30-35 m (where bin 1 = 4-20 m, bin 2 = 21–50 m), but it's comparison with mean and modal dive depths reported by other studies will necessarily be descriptive. However, we believe these variables provide useful statistics for analysis of binned dive data by allowing data to retain their binned-nature rather than assigning an arbitrary and potentially inaccurate number to the parameter of interest.

Examining foraging "effort" from SDR data and future work

Our main objective in collecting dive data was to relate dive behavior to foraging effort in order to test the hypothesis that foraging effort was greater for Kodiak than Southeast seals, if reduced prey availability was a factor in the severe population decline observed near Kodiak Island. However, determining a good variable to describe "foraging effort" is difficult due to limitations imposed by the binned-nature of SDR data. Time wet provides a coarse but useful first look at potential foraging behavior of Alaskan harbor seals, by including shallow water diving, traveling and feeding. Similar to results from other studies (Coltman *et al*. 1997, Lesage *et al*. 1999, Frost *et al*. 2001), harbor seals in Southeast Alaska and around Kodiak Island spend the majority of their time submerged (45-70%) in water less than four meters in depth. The studies of Coltman *et al*. (1997) and Lesage *et al*. (1999) were conducted in the breeding season, when time spent in shallow waters may be biased high due to seals remaining close to shore and engaging in mating and other non-foraging related, shallow-water activities. However, there is evidence for significant foraging by harbor seals during the breeding season in water less than four meters deep (Lesage *et al*. 1999) and for enhanced male reproductive success from shallow-water foraging during the breeding season (Coltman *et al*. 1998). Relating time wet to foraging effort is difficult, however, because this measure includes an unknown proportion of time spent engaged in non-foraging related activities. Harbor seals have been observed playing, resting and sleeping in shallow water (Fedak *et al*. 1988, Bjorge *et al*. 1995) and engaging predominantly in activities related to mating when in shallow waters during the breeding season (Coltman *et al*. 1997). This latter observation implies the capability of time wet to approximate foraging effort may vary with season, sex and age according to the activity budgets of these groups. Furthermore, it is difficult to interpret time-at-depth data in order to examine foraging activity, because it includes time descending and ascending, as well as bottom time of dives.

Whereas time wet does not appear to vary significantly between Kodiak and Southeast seals (Fig. 3a), additional measures that may reflect foraging effort will be examined to consider regional differences. Further analyses of these data will include (1) formal tests for regional effects on time wet, focus, and preferred depth; and (2) inclusion of water depth in statistical analyses to test if regional effects are due solely to differing bathymetric conditions and if effects of other variables (age, sex, season, and time of day) can be explained primarily by movement patterns. We will also (3) test for effects of these variables on other potential descriptors of foraging behavior including: dive frequency for a given depth bin, and preferred dive duration bin, coupled with preferred depth bin. These variables may allow us to infer if Kodiak seals were making more frequent dives of greater duration for a given depth range than Southeast seals.

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Table 1. Adult and subadult harbor seals captured and released with SDRs from 1993-1996 in Southeast Alaska (SE) and Kodiak Island (KO).

ID #	Capture Site	Region	Capture Date	Sex	Age	Mass (kg)	Length (cm)	SDR end dates	Total days operational
93SE02	Gambier Bay	SE	4/5/93	F	A	53.1	123	7/21/93	108
93SE03	Sail Island	SE	4/8/93	M	A	87.7	142	8/25/93	140
93SE04	SW Brothers	SE	4/9/93	M	S	42.6	116	7/29/93	112
93SE07	SW Brothers	SE	4/9/93	M	A	73.6	144	7/29/93	112
93SE09	SW Brothers	SE	4/9/93	M	A	96.5	134	8/14/93	128
93KO01	S. Sitkinak Island	KO	4/22/93	F	A	104.0	152	7/25/93	95
93KO02	S. Sitkinak Island	KO	4/24/93	F	A	115.0	148	7/20/93	88
93KO03	S. Sitkinak Island	KO	4/26/93	F	A	113.8	141	7/12/93	78
93KO04	S. Sitkinak Island	KO	4/26/93	F	S	73.7	136	6/16/93	52
93KO05	S. Sitkinak Island	KO	10/2/93	F	A	62.3	130	1/18/94	109
93SE10	Gambier Bay	SE	9/14/93	M	A	92.7	152	10/1/93	18
93SE15	Gambier Bay	SE	9/17/93	M	A	60.9	124	5/11/94	237
93SE16	Gambier Bay	SE	9/17/93	M	A	62.2	129	4/11/94	207
93SE18	Gambier Bay	SE	9/17/93	M	A	67.4	137	10/5/93	19
93SE19	Gambier Bay	SE	9/17/93	F	A	43.0	117	4/27/94	223
93SE20	Gambier Bay	SE	9/17/93	M	A	44.4	118	4/21/94	217
94SE02	Price Island	SE	9/13/94	F	A	74.4	135	4/20/95	220
94SE03	Price Island	SE	9/13/94	M	A	93.1	144	5/1/95	231
94SE05	Price Island	SE	9/13/94	F	A	56.2	132	2/12/95	153
94SE07	Price Island	SE	9/13/94	M	A	87.9	-	7/13/95	304
94SE08	Price Island	SE	9/13/94	F	A	77.0	151	5/11/95	241
94SE09	Price Island	SE	9/13/94	M	A	80.9	144	4/19/95	219
94KO01	Ugak Bay	KO	10/5/94	M	A	87.8	149	4/21/95	199
94KO02	Ugak Bay	KO	10/5/94	M	A	93.3	140	7/19/95	288
94KO04	Ugak Bay	KO	10/6/94	F	S	31.7	94.5	1/19/95	106
94KO08	Kiliuda Bay	KO	10/8/94	M	A	47.7	117	6/3/95	239
94KO09	Kiliuda Bay	KO	10/8/94	F	S	35.8	107	6/23/95	259
95KO01	Uganik Passage	KO	3/29/95	M	A	85.4	146	7/29/95	123
95KO02	Uganik Passage	KO	3/29/95	F	S	48.9	120	6/7/95	71
95KO03	Uganik Passage	KO	3/29/95	F	A	113.3	148	6/14/95	78
95KO04	Uganik Passage	KO	3/29/95	M	S	50.1	110	5/24/95	57
95KO05	Uganik Passage	KO	3/29/95	F	S	57.2	114	7/8/95	102
95SE01	Price Island	SE	4/19/95	M	A	56.0	125	7/13/95	86
95SE03	Price Island	SE	4/19/95	F	A	68.9	127	7/7/95	80
95SE07	Price Island	SE	4/19/95	F	S	36.2	110	7/4/95	77
95SE09	Price Island	SE	4/19/95	F	S	30.6	103	6/16/95	59
95SE17	Price Island	SE	4/19/95	F	A	93.3	138	7/21/95	94
95KO09	Upper Ugak Bay	KO	10/9/95	F	S	53.7	120	6/4/96	240
95KO10	Upper Ugak Bay	KO	10/9/95	M	S	30.7	98	5/27/96	232
95KO12	Upper Ugak Bay	KO	10/9/95	F	A	75.0	134	6/27/96	263
95KO13	Upper Ugak Bay	KO	10/9/95	M	A	93.3	151	6/17/96	253
95KO14	Upper Kiliuda Bay	KO	10/10/95	F	A	47.2	122	2/28/96	142
95KO15	Upper Kiliuda Bay	KO	10/10/95	F	S	31.4	96	5/14/96	218
95SE20	Vixen Island	SE	9/21/95	M	A	70.2	140	4/20/96	213
95SE21	Vixen Island	SE	9/21/95	F	A	80.6	142	4/28/96	221
95SE24	Vixen Island	SE	9/22/95	F	S	31.3	108	5/13/96	235
95SE25	Vixen Island	SE	9/22/95	F	A	54.4	132	5/30/96	252
96SE01	Vixen Island	SE	9/24/96	M	A	78.5	145	1/9/97	108

Table 1. Cont.

ID #	Capture Site	Region	Capture Date	Sex	Age	Mass (kg)	Length (cm)	SDR end dates	Total days operational
96SE03	Vixen Island	SE	9/24/96	F	A	70.3	132	5/13/97	232
96SE04	Vixen Island	SE	9/26/96	M	S	45.4	115	6/19/97	267
96SE05	Vixen Island	SE	9/26/96	M	A	67.6	132	6/17/97	265
96SE08	Vixen Island	SE	9/26/96	F	A	55.3	122	11/1/96	37
96SE10	Outer Krugloi	SE	9/27/96	M	S	38.6	107	3/8/97	163
96SE14	Vixen Island	SE	9/28/96	F	S	34.4	105	12/29/96	93
96SE15	Vixen Island	SE	9/28/96	M	S	48.0	123	6/3/97	249
96KO02	Uganik Passage	KO	10/15/96	M	A	87.4	148	8/6/97	296
96KO03	Uganik Passage	KO	10/15/96	M	A	108.3	157	5/29/97	227
96KO06	S. Arm Uganik Bay	KO	10/17/96	M	A	69.7	135	3/18/97	153
96KO09	S. Arm Uganik Bay	KO	10/17/96	M	A	116.6	156	6/1/97	228
96KO12	S. Arm Uganik Bay	KO	10/17/96	M	S	45.8	112	4/12/97	178
96KO14	S. Arm Uganik Bay	KO	10/17/96	M	A	76.7	136	12/25/96	70
96KO15	S. Arm Uganik Bay	KO	10/17/96	M	S	38.1	106	1/30/97	106

Table 2. Summary of dive data obtained from SDRs deployed on adult and subadult harbor seals near Kodiak Island and in Southeast Alaska, 1993-1996. Dive depth and duration were summarized as proportion of dives per bin averaged over histograms. Time-at-depth data were available only from instruments deployed from 1995-1996. Finer scale time-at-depth data were available only from instruments deployed in 1996, where bins 0-4 m and 5-20 m were used.

	Kodiak					Southeast				
	All	Female	Male	Adult	Subadult	All	Female	Male	Adult	Subadult
Dive Frequency										
N histograms	*10,366*	*3,958*	*6,408*	*7,466*	*2,900*	*14,286*	*6,286*	*8,000*	*12,414*	*1,872*
N seals	*28*	*14*	*14*	*17*	*11*	*34*	*15*	*19*	*26*	*8*
N dives	*541,771*	*223,627*	*318,144*	*358,440*	*183,331*	*687,237*	*299,839*	*387,398*	*572,582*	*114,655*
Mean (# dives/6 hr)	52.3	56.5	49.6	48.0	63.2	48.1	47.7	48.4	46.1	61.2
CV	0.80	0.82	0.78	0.78	0.81	0.84	0.73	0.93	0.88	0.61
Range (# dives/6 hr)	1 - 356	1 - 356	1 - 301	1 - 301	1 - 356	1 - 375	1 - 256	1 - 375	1 - 375	1 - 227
Dive Depth Bin										
4-20 m	55.0	49.2	58.7	60.4	41.3	47.8	48.2	47.5	47.9	46.9
21-50 m	30.9	35.0	28.4	30.3	32.5	12.5	16.2	9.6	11.6	18.4
51-100 m	12.5	14.9	11.0	8.0	24.0	26.5	25.5	27.2	27.0	22.9
101-150 m	1.3	0.9	1.6	1.1	1.7	9.2	8.6	9.8	9.4	8.3
151-200 m	0.3	0.1	0.4	0.2	0.4	3.3	1.5	4.7	3.3	3.1
>200 m	0.0	0.0	0.1	0.0	0.1	0.7	0.0	1.2	0.7	0.4
Dive Duration Bin										
N histograms	*10,434*	*4,057*	*6,377*	*7,484*	*2,950*	*14,208*	*6,269*	*7,939*	*12,324*	*1,884*
N seals	*28*	*14*	*14*	*17*	*11*	*34*	*15*	*19*	*26*	*8*
N dives	*530,363*	*218,115*	*312,248*	*354,679*	*175,684*	*650,528*	*299,646*	*350,882*	*533,798*	*116,730*
0-2 min	42.4	36.9	45.9	46.0	33.1	40.0	39.4	40.4	39.8	41.0
>2-4 min	32.8	40.8	27.7	27.8	45.4	24.2	24.4	24.0	22.2	37.0
>4-6 min	17.4	18.5	16.7	16.9	18.5	19.1	18.8	19.3	19.5	16.6
>6-8 min	5.2	2.8	6.7	6.4	2.0	9.7	11.0	8.6	10.6	3.7
>8-10 min	1.4	0.5	2.0	1.8	0.4	3.8	4.2	3.5	4.3	0.5
>10 min	0.9	0.6	1.2	1.0	0.7	3.3	2.2	4.1	3.6	1.3
Time at Depth										
N histograms	*7,621*	*2,702*	*4,919*	*5,278*	*2,343*	*6,556*	*3,845*	*2,711*	*4,905*	*1,651*
N seals	*17*	*6*	*11*	*9*	*8*	*17*	*10*	*7*	*10*	*7*
Prop time dry [a]	27.0	28.0	26.5	27.2	26.6	27.7	28.0	27.2	27.8	27.3
0-20 m	79.0	76.9	80.1	81.6	73.1	65.9	68.5	62.3	66.4	64.6
21-50 m	15.7	18.7	14.1	14.3	18.9	12.3	13.3	11.0	10.7	17.0
51-75 m	4.1	3.9	4.3	3.0	6.7	8.3	7.8	9.0	7.8	9.9
76-100 m	0.7	4.3	0.8	0.6	0.9	5.2	4.5	6.1	5.7	3.7
101-150 m	0.4	0.0	0.6	0.4	0.4	6.7	5.2	8.9	7.8	3.7
151-200 m	0.1	0.0	0.7	0.1	0.1	1.3	0.6	2.3	1.5	0.9
201-250 m	0.0	0.0	0.0	0.0	0.0	1.4	0.1	0.3	0.2	0.0
>250 m	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1996 only [b]: 0 – 4 m	*84.7*	**	*84.7*	*85.1*	*81.1*	*75.3*	*76.6*	*74.7*	*78.4*	*68.9*
1996 only [b]: 5- 20 m	*15.3*	**	*15.3*	*14.9*	*18.9*	*24.7*	*23.4*	*25.3*	*21.6*	*31.1*
Maximum Depth										
N dives	*2,558*	*996*	*1,562*	*1,913*	*645*	*3,393*	*1,573*	*1,820*	*2,960*	*433*
Mean	76.4	72.1	79.2	73.0	86.5	203.2	155.7	244.2	211.9	143.2
Maximum	368	368	320	320	368	508	468	508	508	504
CV	0.60	0.62	0.59	0.62	0.55	0.52	0.41	0.48	0.49	0.67

[a] Prop time dry: Mean proportion of time the conductivity sensor was dry (seal hauled-out or not submerged at the surface) per six hour period.
[b] 1996 only: Summarized as mean proportion time in bins 0-4 m and 5-20 m of the total time spent from 0-20 m.
** No females were tagged with SDRs in Kodiak in 1996.

Table 3. Covariance parameter estimates from final repeated measures mixed models of time wet, focus, and preferred dive depth. Parameters were seal (individual variation), autocorrelation, and final residual (final residual variation after fixed effects, seal and autocorrelation were accounted for). The proportion of residual variance (after fitting fixed effects only) explained by each parameter is in parentheses. Range indicates the estimated number of days autocorrelation effects persisted.

Model	Covariance Parameter Estimates (*Proportion of Residual Variance*)						
	Seal		Autocorrelation		Final Residual		Range (Days)
Kodiak							
Time wet	322.76	*(0.02)*	1263.49	*(0.10)*	11640.98	*(0.88)*	12.47
Focus – Majority time wet	0.0033	*(0.07)*	0.0085	*(0.17)*	0.0382	*(0.76)*	37.88
Focus - Any time wet	0.0036	*(0.07)*	0.0043	*(0.08)*	0.0443	*(0.85)*	52.76
Preferred Depth – Majority time wet	0.00	*(0.00)*	0.01	*(0.25)*	0.03	*(0.75)*	41.41
Preferred Depth - Any time wet	0.12	*(0.27)*	0.12	*(0.27)*	0.21	*(0.47)*	25.04
Southeast Alaska							
Time wet	178.96	*(0.02)*	665.59	*(0.07)*	8815.12	*(0.91)*	17.74
Focus – Majority time wet	0.0016	*(0.03)*	0.0057	*(0.12)*	0.0405	*(0.85)*	17.58
Focus - Any time wet	0.0051	*(0.09)*	0.0088	*(0.15)*	0.0455	*(0.77)*	9.98
Preferred Depth – Majority time wet	0.22	*(0.16)*	0.62	*(0.46)*	0.50	*(0.37)*	14.19
Preferred Depth – Any time wet	0.11	*(0.11)*	0.29	*(0.29)*	0.60	*(0.60)*	40.93

Table 4. Diurnal and seasonal estimates of the number of minutes harbor seals from Kodiak Island and Southeast Alaska were submerged (time wet) from repeated measures analyses. Time-at-depth data were only available from SDRs deployed in 1995-1996 (n = 35 individuals). Estimates are in minutes (out of 360 minutes possible), and are relative to the intercept value for each region that is based on the six-hour evening period in December.

	Kodiak[a]			Southeast[b]		
Effect	Estimate	SE	P(t)	Estimate	SE	P(t)
Intercept	289.331	12.959	<0.001	258.634	12.693	<0.001
Month						
January	-38.899	16.600	0.019	-22.794	17.353	0.189
February	-33.743	16.543	0.042	-11.688	17.559	0.506
March	-47.046	16.088	0.004	-2.520	16.659	0.880
April	-35.856	15.527	0.021	-20.402	15.406	0.186
May	-47.473	15.418	0.002	-29.489	15.209	0.053
June	-58.894	19.000	0.002	-40.083	16.256	0.014
July	-74.708	25.154	0.003	-84.644	22.657	<0.001
September				-17.873	20.229	0.377
October	-18.583	17.553	0.290	-10.099	13.999	0.471
November	-37.259	15.775	0.018	8.476	16.147	0.600
December	0			0		
Time of Day [c]						
Night	25.231	9.455	0.008	13.171	7.823	0.093
Morning	-20.125	8.597	0.019	-17.812	7.025	0.011
Day	-45.395	8.251	<0.001	-5.231	7.236	0.470
Evening	0			0		

[a] $N_{histograms}$ (Kodiak) = 1321
[b] $N_{histograms}$ (Southeast) = 1338
[c] Time of Day: Night = 2100-0300, morning = 0300-0900, day = 0900-1500, evening = 1500-2100

Table 5. Diving focus estimates for harbor seals in Kodiak and Southeast Alaska from repeated measures analyses. Focus was calculated using "D" from Simpson's Diversity Index (see text). Separate analyses were conducted for "any time wet" data (all data included) and "majority time wet" data (data from histograms where time wet > 180 minutes). The possible range of "D" included 0.167 (dives evenly distributed among six depth bins; unfocused diving) to 1.0 (all dives in one bin). We assumed focus values (D) > 0.5 represented "focused" diving (dives were more common in one depth bin). Intercept values represent focus estimates for the combination of factors having zero parameter values.

Kodiak				Southeast			
Effect	Estimate	SE	P(t)	Effect	Estimate	SE	P(t)
Any time wet [a]				Any time wet [c]			
Intercept	0.563	0.040	<0.001	Intercept	0.574	0.020	<0.001
Sex/Age-Class				Time of Day			
Adult Females	0.206	0.058	<0.001	Night	0.025	0.014	0.077
Subadult Females	0.025	0.049	0.603	Morning	0.007	0.010	0.503
Adult Males	0.086	0.045	0.055	Day	0.091	0.012	<0.001
Subadult Males	0			Evening	0		
Time of Day				Subregion			
Night	0.034	0.016	0.035	SE1	0.025	0.014	0.069
Morning	0.015	0.014	0.260	SE2	-0.061	0.030	0.039
Day	0.113	0.014	<0.001	SE8	0		
Evening	0						
Majority time wet [b]				Majority time wet [d]			
Intercept	0.555	0.030	<0.001	Intercept	0.433	0.034	<0.001
Age-Class				Sex			
Adults	0.091	0.038	0.016	Females	0.073	0.028	0.010
Subadults	0			Males	0		
Time of Day				Month			
Night	0.026	0.018	0.133	January	-0.043	0.040	0.286
Morning	0.006	0.016	0.698	February	-0.064	0.043	0.138
Day	0.142	0.016	<0.001	March	-0.036	0.042	0.388
Evening	0			April	0.015	0.038	0.698
				May	0.047	0.038	0.220
				June	0.065	0.042	0.121
				July	0.137	0.064	0.033
				September	0.057	0.050	0.251
				October	0.050	0.035	0.158
				November	0.045	0.038	0.236
				December	0		
				Time of Day			
				Night	0.051	0.017	0.002
				Morning	0.001	0.016	0.938
				Day	0.106	0.016	<0.001
				Evening	0		

[a] $N_{histograms}$ (Kodiak) = 1778
[b] $N_{histograms}$ (Kodiak) = 1200
[c] $N_{histograms}$ (Southeast) = 2920
[d] $N_{histograms}$ (Southeast) = 1276

Table 6. Preferred dive depth bin estimates for adult and subadult harbor seals near Kodiak Island and Southeast Alaska from repeated measures analyses. Separate analyses were conducted for "any time wet" data (all data included) and "majority time wet" data (data from histograms where time wet > 180 minutes). Data included only histograms in which diving was focused (D > 0.5).

Kodiak				Southeast			
Effect	Estimate	SE	P(t)	Effect	Estimate	SE	P(t)
Any time wet [a]				Any time wet [b]			
Intercept	1.687	0.117	<0.001	Intercept	2.289	0.130	<0.001
Age-Class				Month			
Adults	-0.386	0.155	0.013	January	0.174	0.141	0.217
Subadults	0			February	0.147	0.159	0.353
				March	-0.384	0.163	0.018
				April	-0.755	0.156	<0.001
				May	-1.043	0.164	<0.001
				June	-1.070	0.180	<0.001
				July	-1.006	0.218	<0.001
				August	-0.883	0.341	0.010
				September	-0.801	0.163	<0.001
				October	-0.388	0.143	0.007
				November	-0.441	0.130	0.001
				December	0		
				Time of Day			
				Night	-0.267	0.059	<0.001
				Morning	-0.169	0.041	<0.001
				Day	-0.212	0.044	<0.001
				Evening	0		
Majority time wet [c]				Majority time wet [d]			
Intercept	0.716	0.019	<0.001	Intercept	2.912	0.241	<0.001
Age-Class				Month			
Adults	0.079	0.023	0.001	January	-0.019	0.285	0.946
Subadults	0			February	-0.635	0.305	0.038
				March	-1.105	0.297	<0.001
				April	-1.401	0.275	<0.001
				May	-1.614	0.284	<0.001
				June	-1.826	0.318	<0.001
				July	-1.740	0.419	<0.001
				September	-1.716	0.334	<0.001
				October	-0.867	0.258	0.001
				November	-1.026	0.266	<0.001
				December	0		

[a] $N_{histograms}$ (Kodiak) = 1565
[b] $N_{histograms}$ (Kodiak) = 1062
[c] $N_{histograms}$ (Southeast) = 2580
[d] $N_{histograms}$ (Southeast) = 908

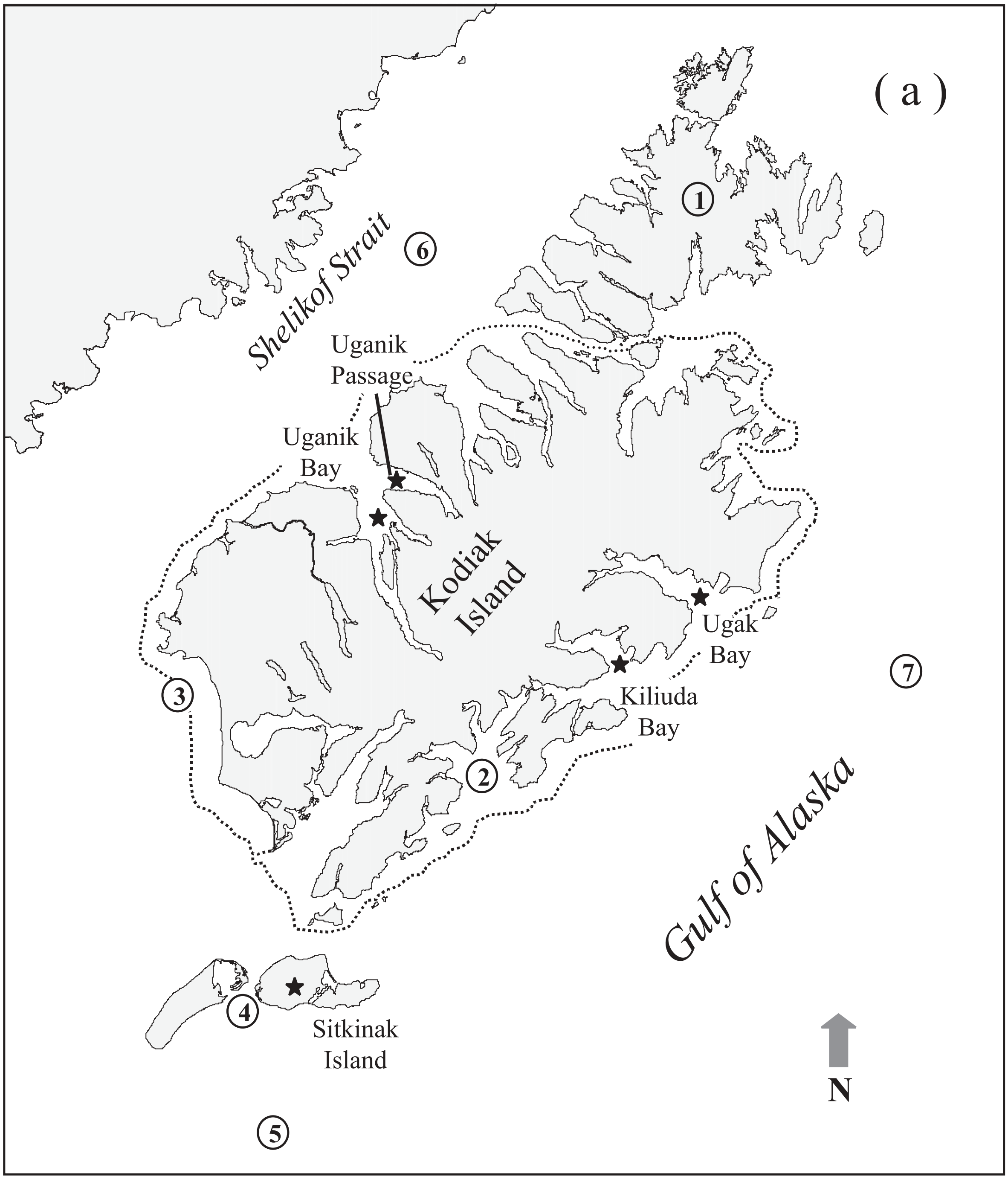


Fig. 1. Harbor seal capture sites where SDRs were deployed from 1993 to 1996 around Kodiak Island, Alaska. Capture sites are marked with stars and labeled. Locations of seals from SDRs were grouped into seven subregions, shown in white circles; KO1-KO4 nearshore, and KO5-KO7 offshore. Most of these locations (91.2%) occurred in subregions KO2 (near-shore along the south coast of Kodiak Island) and KO3 (near-shore along the north coast of Kodiak Island, delineated with dotted line).

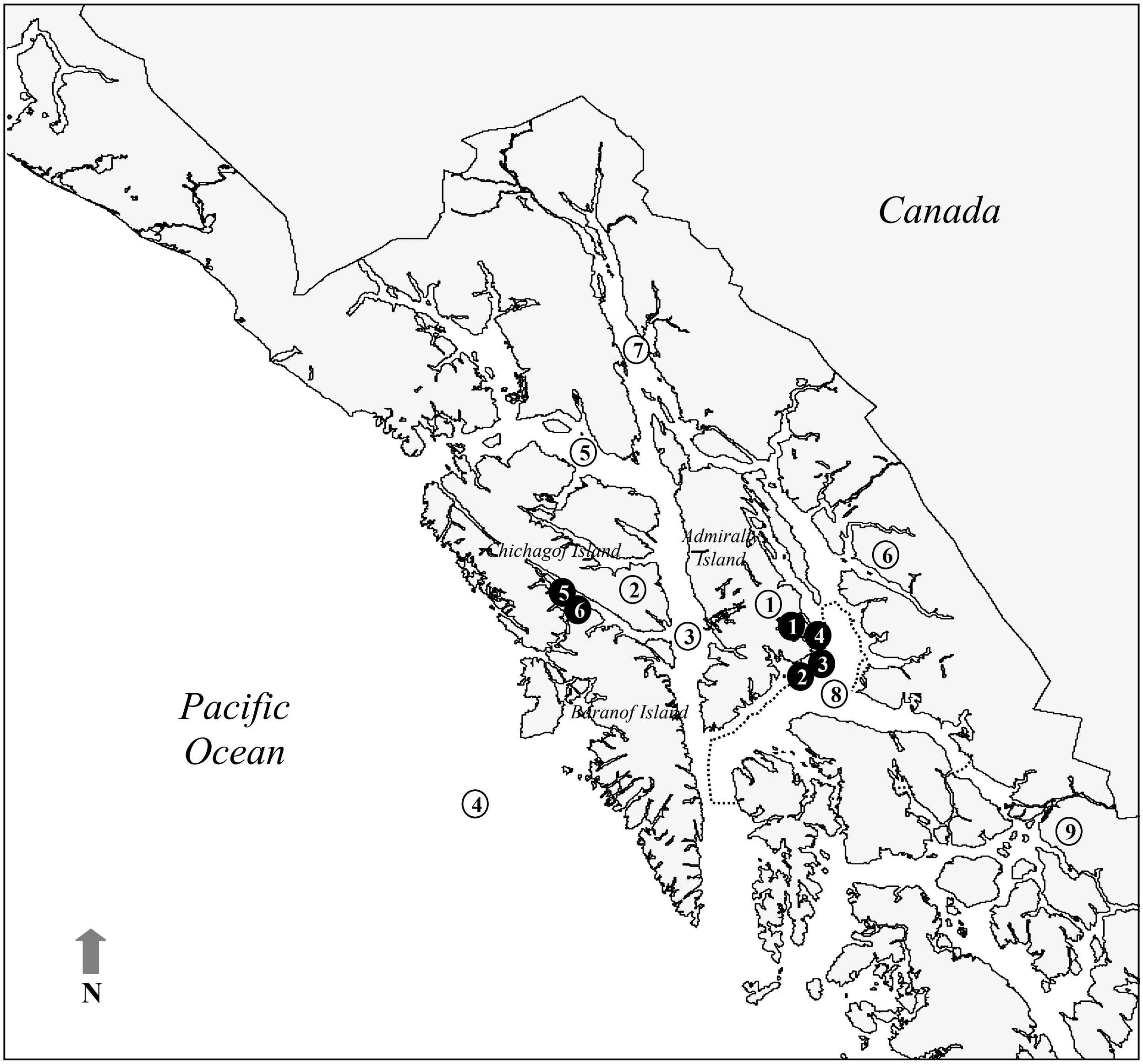
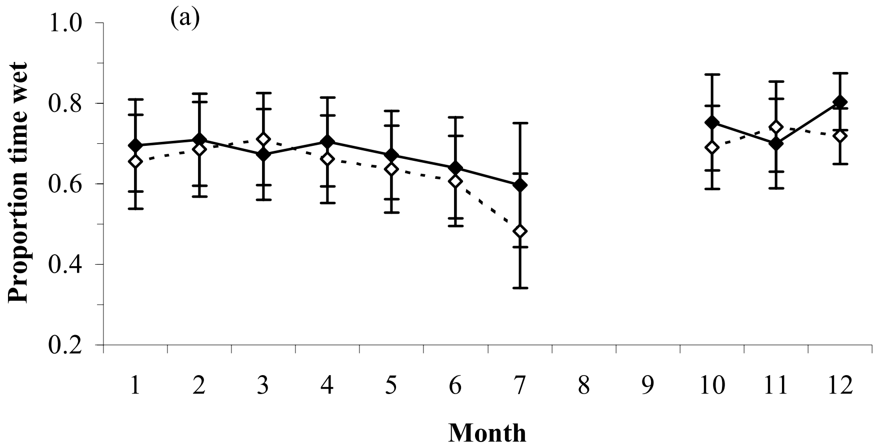


Fig. 2. Harbor seal capture sites where SDRs were deployed from 1993 to 1996 around Southeast Alaska. Capture sites are shown in black circles with white numbers; 1=Gambier Bay, 2=SW Brothers, 3=Sail Island, 4=Price Island, 5=Vixen Island, and 6=Krugloi Island. Locations of seals from SDRs were grouped into nine subregions, shown in white circles with black numbers. Most of theses locations (96.4%) occurred in subregions SE1 (near-shore around the coast of Admiralty Island), SE2 (near-shore around the coasts of Chichagof and Baranof Islands), and SE8 (Frederick Sound, delineated with dotted line).



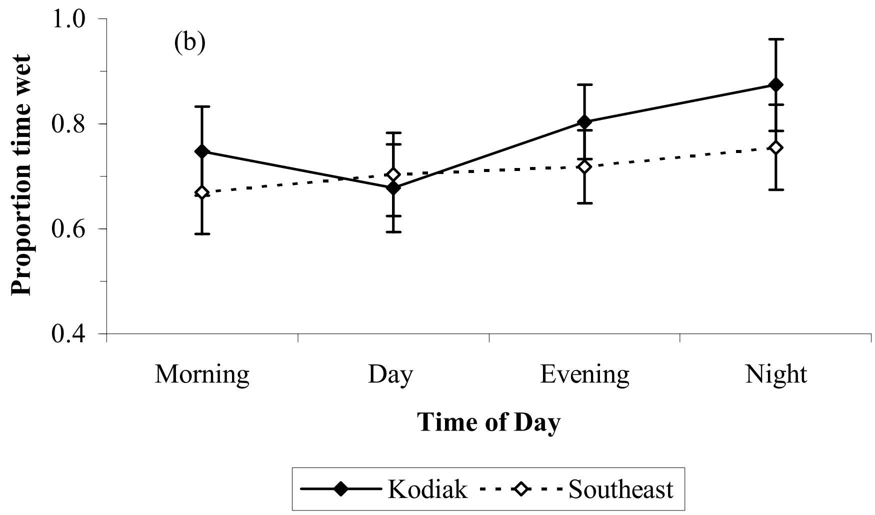


Fig. 3. Seasonal (a) and diurnal (b) estimates of the proportion of time harbor seals were submerged (i.e., "time wet") based on repeated measures analyses of time-at-depth data from SDRs deployed on adult and subadult harbor seals from Kodiak Island and Southeast Alaska during 1995-1996. Proportions were calculated from estimates of the number of minutes harbor seals were wet (Table 4) during a 360 minute period. Estimates were standardized to the zero parameter estimates in Table 4; Fig. 3a is standardized to the evening period and Fig. 3b is standardized to December. Time of day periods were: Morning = 0300-0900 hrs, Day = 0900-1500 hrs, Evening = 1500-2100 hrs, Night = 2100-0300 hrs. Error bars are 95% confidence intervals.

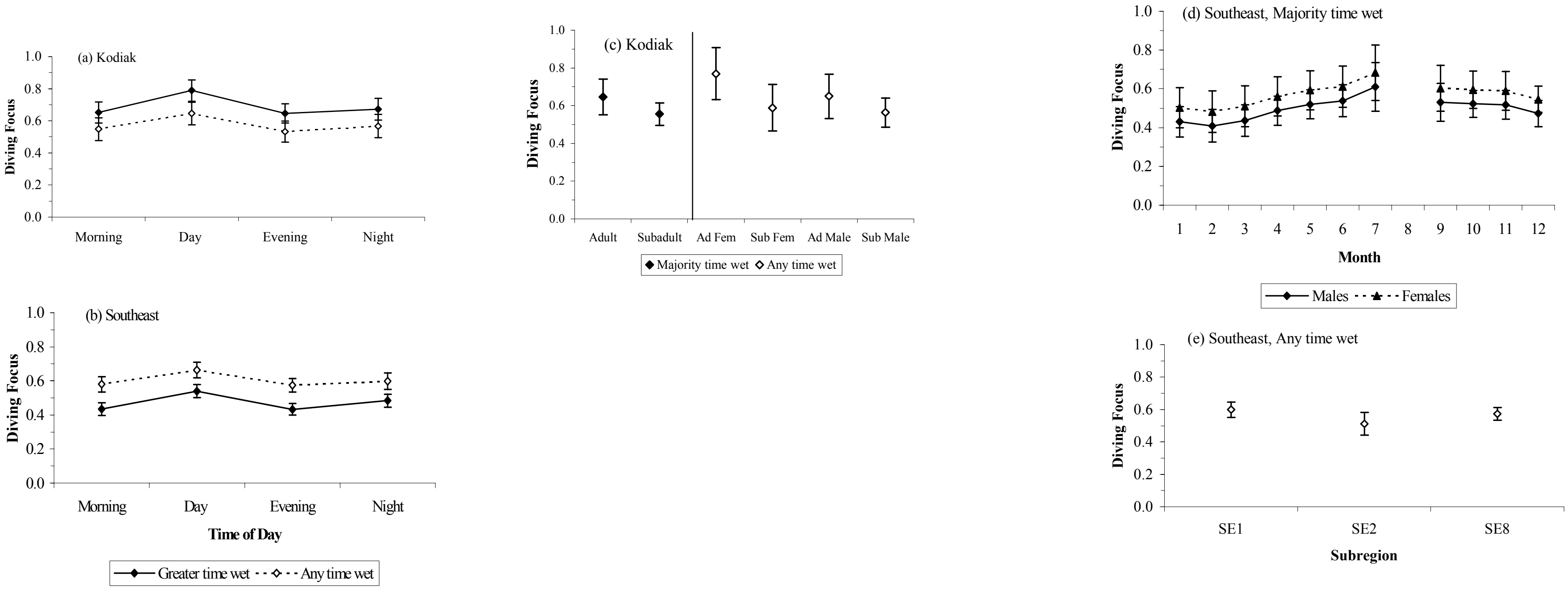


Fig. 4. Effects of time of day (a,b), age-class (c), sex (c,d), season (d), and subregion (e) on diving focus of adult and subadult harbor seals from Kodiak and Southeast Alaska, 1993-1997. Diving focus was calculated using Simpson's diversity index to describe the diversity of bins used by seals; focus values > 0.50 indicate that diving was more prevalent in one bin (see text). Diving focus was examined for two datasets for both Kodiak and Southeast: (1) "any time wet", including all data regardless of time spent under water, and (2) "majority time wet", including only histograms from periods where >180 minutes (or 50% of the time) was spent under water. Time of day: Morning = 0300-0900 hrs, Day = 0900-1500 hrs, Evening = 1500-2100 hrs, Night = 2100-0300 hrs. Error bars are 95% confidence intervals. Estimates were standardized to the zero parameter estimates in Table 5.

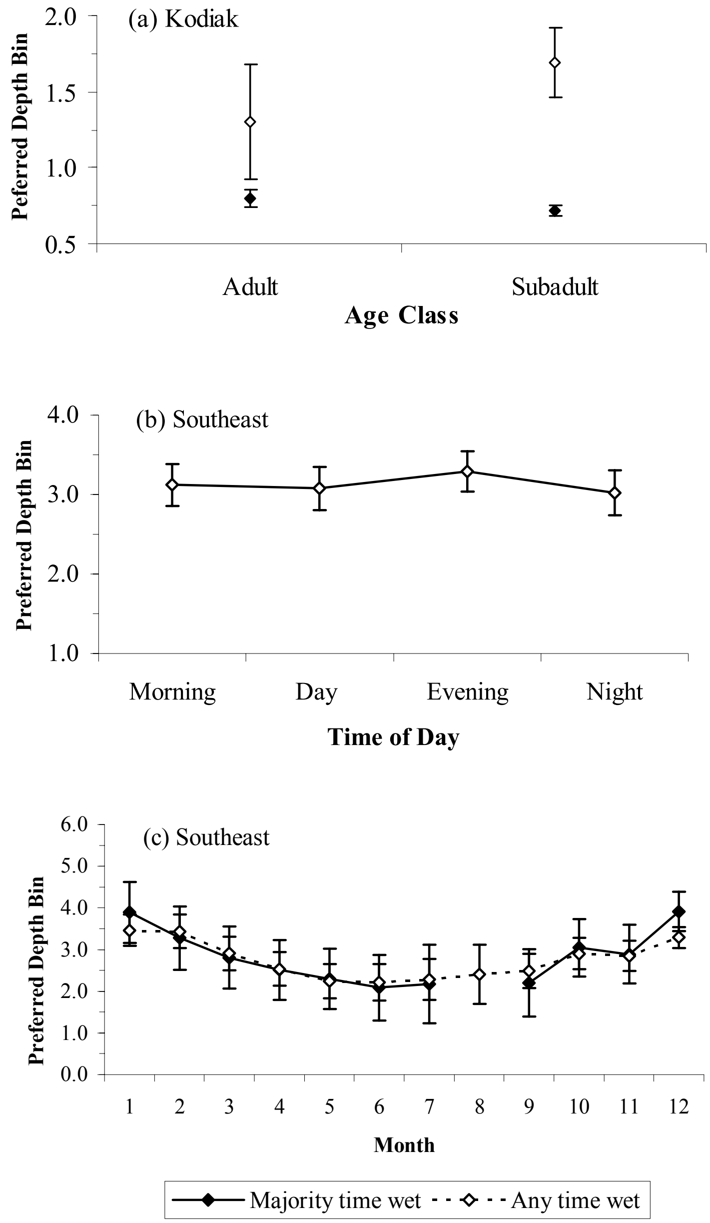


Fig. 5. Effects of age-class (a), time of day (b), and season (c) on preferred dive depth bin of adult and subadult harbor seals from Kodiak and Southeast Alaska, 1993-1996. Preferred depth bin describes the bin in which dives were most prevalent during periods of focused diving (included data in which diving focus “D” was > 0.5). Depth bins were Bin 1 = 4-20 m, Bin 2 = 21-50 m, Bin 3 = 51-100 m, Bin 4 = 101-150 m, Bin 5 = 151-200 m, and Bin 6 = >200 m. Two datasets for both regions (Kodiak and Southeast) were examined: (1) “any time wet”, including all data regardless of time spent under water, and (2) “majority time wet”, including only histograms from periods where >180 minutes (or 50% of the time) was spent under water. Time of day: Morning = 0300-0900 hrs, Day = 0900-1500 hrs, Evening = 1500-2100 hrs, Night = 2100-0300 hrs. Error bars are 95% confidence intervals. Estimates from repeated measures mixed models were standardized to the zero parameter estimates in Table 6.